EXPERIMENTAL STUDIES IN THE TAXONOMY OF THE SPECIES OF ELYTRARIA IN WEST AFRICA

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O. B. DOKOSI

In West Tropical Africa, four kinds of Elytraria occur: One is an acaulous perennial plant bearing a rosette of radical, mostly spreading lyrate leaves. Another is a cauliferous, erect, unbranched or sparingly branched annual plant, bearing more or less spathulate-acute leaves. The third is a much branched, prostrate, creeping plant, bearing more or less elliptic leaves. And the fourth is also acaulous but annual plant, bearing radical obovate leaves.

In a recent taxonomic and cytological study of this genus, J. K. Mor-TON (Revista Biol. 1: 49-58, 1956) showed that the first of the above three plants was the same as Elytraria lyrata VAHL, the second, the same as E. marginata VAHL. He described the third as a new species and named it E. maritima J. K. MORTON.

MORTON also clearly showed that the earlier determination of the first two kinds of plants as E. acaulis (L. f.) LINDAU (in F.W.T.A. ed. 1, 2, 261, 1931) was incorrect as the true E. acaulis, an Indian plant, was clearly distinct from any of the above plants. On the basis of this, Bremekamp's treatment (in Reinwardtia 3: 249, 1955) of the second kind of plant as E. acaulis and the first kind as E. acaulis var. lyrata is also to be rejected.

In the most recent account of the West African species of this genus, however, Heine (in F.W.T.A. ed. 2, 2: 418, 1963) recognised only two species: i) E. marginata VAHL and E. maritima J. K. MORTON. Under E. marginata VAHL of which E. lyrata VAHL was regarded a synonym, Heine added the following note: "A polymorphic species which is accepted here in a broad sense". In the case of E. maritima, he expressed the view that it is "a local race of E. marginata, described in specific rank".

The first three kinds of Elytraria occur in Ghana and the fourth in the Ivory Coast¹. The study of these plants has been based on specimens collected from these two countries, although herbarium specimens from other parts of Africa and India have also been examined. The herbarium specimens of E. marginata obtained from Nigeria F.H.I. 23962, F.H.I. 15511, and J.P.M.

¹ Recently, E. ivorensis has been recorded also in Ghana, Atewa Range F. R. by A. A. ENT1 nr. G C 37441 (GC).

Brenan No. 9237, F.H.I. 58972) are similar to those from Ghana. So is the herbarium specimen obtained from the Congo (Ex Herbario Botanici Yan-

gambiensis, L. Coussaint 2279).

All these differ from the herbarium specimen of *E. acaulis* LINDAU obtained from India Central National Herbarium, Flora of Nagarjuma, Konda Valley No. 9635).

HABITAT CONDITIONS AND DISTRIBUTION

Observations in the field and field notes on the relevant herbarium specimens from Ghana Herbarium and from other herbaria show that each of

the four forms of Elytraria has a distinct ecological niche.

E. marginata is widespread in the forest regions in cocoa and coffee farms and in other parts of the forest where trees afford shade. The mean annual rainfall is 50—70 in. and the Relative Humidity ranges from 70 to 100%. The soil is rich in humus. E. lyrata is mainly a dry zone plant and grows in the coastal scrub and grassland where the mean annual rainfall is 30—40 in. The Relative Humidity is low and the surface of the soil is baked hard in the dry season.

E. maritima occurs along the western coast of Ghana and extends into the adjacent forests of the Ivory Coast. The mean annual rainfall is

70-80 in. This is the region of heaviest rainfall in Ghana.

E. ivorensis Dokosi which has just been described (description in print) has so far been recorded only from the forest region of the Ivory Coast.

J. K. MORTON (l. c.) gives the following distribution of the first three types of *Elytraria* as follows:

E. lyrata: Ghana, Congo and Angola.

E. marginata: Sierra Leone, Liberia, Ghana, Republic of Togo, Nigeria, Cameroons, Fernando Po, Sao Tome, Principe, Spanish Guinea, Gabon, Congo and Angola.

E. maritima: Ivory Coast, Ghana.

METHOD AND MATERIAL

The following methods were used in the course of this study:

1. Collateral cultivation in a neutral and uniform habitat by transplantation.

2. Crossing experiments between all the four kinds.

3. Comparison of herbarium specimens of those plants collected from their natural habitats.

Cultivation by transplanting of the first three types started in September 1964. For this purpose, 50—60 living plants were selected from each population. They were placed in polythene bags previously wetted with water. These plants were cultured in wooden boxes containing John Innes

Potting Compost after the soil had been carefully washed from the roots. The wooden boxes which measured $46\times30\times12$ cm were placed on concrete platforms in the greenhouse and the plants watered twice or thrice per week. Some of the plants were cultured on beds in the University Botanical Garden. Plants of *E. ivorensis* Dokosi were obtained from the Ivory Coast University Botanical Garden in Abidjan with the kind permission of Professor L. Aké Assi in April 1968. They were collected from their natural habitats and cultured in that garden. The plants brought from Abidjan and planted in the Legon Botanical Garden produced seeds and several generations are being raised from seeds. The plants of *E. ivorensis* being raised from seeds of the original plants resemble their parents in every respect, i. e. they are breeding true to their morphological characters.

All the four types are still being grown at Legon. They have spread as weeds in the green house, in pots planted with other plants and in the Botanical Garden. Wherever they are found, there is no difficulty in identifying

one form from the other.

DESCRIPTION OF THE PLANTS

Elytraria lyrata VAHL is an acaulous perennial plant bearing a rosette of radical lyrate leaves (Fig. 1). The first 2-4 first formed leaves at the basal part of the rosette are obovate-cuneate, more or less entire and smaller than those formed later. All the later formed ones are lyrate and vary in size from (15)-40-105(-150) mm in length and (10)-20-40(-55) mm in breadth at the broadest part. The hairs are confined to the petiole and the midrib and the lamina is glabrous. After germination the epicotyl undergoes extremely little elongation, so that the distance between the cotyledonary node and the next node above it is hardly more than 2-3 mm in length. Stem elongation ceases and a rosette of leaves produced. The result is a seemingly stemless plant bearing a rosette of apparently radical leaves, spreading on the surface of the soil. The terminal bud produces leaves, but at the time of flowering, it develops directly into a narrow long-stalked cylindrical spike. One or two axillary buds usually from the periphery also often give rise to a corresponding number of rosettes which produce their own adventitious roots at the base. During the flowering period they develop directly into spikes as do the terminal buds.

After the maturity of the flowers all the spikes and the leaves die down and wither, but the rootstock persists and remains dormant beneath the surface of the soil. Shortly after this, one or more axillary buds develop into shoots, bearing, like their parent plants a rosette of leaves and adventitious roots. These shoots undergo the same life-cycle as the parent plants and in this way perennation takes place.

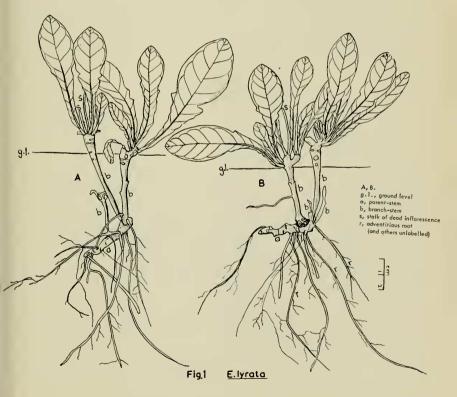
The inflorescence is a spike and the corolla is bilabiate. In this type of *Elytraria* each of the three lobes of the lower lip is markedly emarginate and

in the open flower all the three lobes lie flat in the same plane, and look like three short-armed Y's. The filament is terrete. The anthers are two-celled and the cells are unequal in size. The connective is prolonged into a hook-like appendage on top of the anthers. This feature is characteristic of this form of *Elytraria* only and does not occur in the other three forms.

BENTHAM and HOOKER f. (in Gen. Pl. 2: 1073, 1876) described the stigma thus: 'stylus apice brevissimo 2-lobus'. I. H. BURKILL and C. B. CLARKE (in F.T.A. 5: 27, 1900), JOHRI and SINGH (in Bot. Notiser 112: 227, 1959) also described the style in the following terms: "The style passes along the posterior side of the flower and ends in two laterally expanded unequal stigmas." In the species investigated, two types of stigma have been found: In *E. lyrata* the distal portion of the style expands into a complanate more or less reniform stigma. In the other forms it expands into a lanceolate stigma.

The capsule is narrowly cylindrical with straight sides and blunt apex; it is glabrous and varies from 4—6 mm in length. In E. lyrata it is tinted red at the apex. The seeds which are 0.36—0.55 mm \times 0.31—0.46 mm are coarsely wrinkled, pale brown, glossy with small lighter coloured granula-

tions on the surface.



E. marginata is an erect annual with an unbranched or sparingly branched distinct aerial stem (Fig. 2). The first whorl of leaves is carried 4—20 cm above the soil surface. The terminal bud develops into a terminal spike after the production of the first whorl of leaves. It elongates and produces flowers. Normally a few more buds from the axils of the inner leaves of the whorl also develop into spikes.

The leaves which are distinctly different from those of *E. lyrata* are more or less spathulate with usually a broadly acute tip and more or less entire to faintly crenulate margin. Towards the base of each leaf, the lamina usually shows a few faint transverse foldings on both sides of the midrib. These at the corresponding sides of the margin, give a slight wavy appearance, but are distinctly different from the lobed margin of the lower part of the lyrate leaves of *E. lyrata*. In the unbranched plant, the single internode 4—20 cm, bears a rosette of 5—10 leaves. These vary in size from (15—)

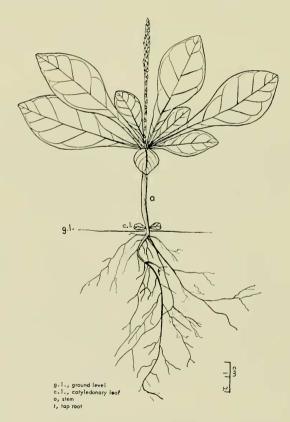
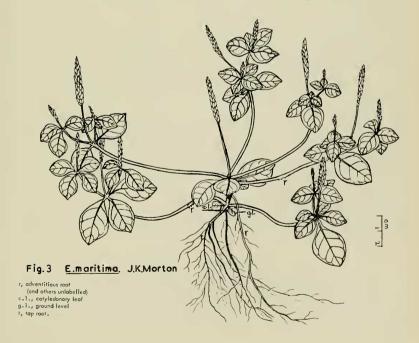


Fig.2 <u>E.marginata</u>

45—100 (—145) mm in length and (10—) 25—40 (—45) mm in breadth at the broadest part. In the branched plants each plant consists of 3—8 cm long internode and bears a single terminal rosette of 5—10 leaves which are smaller than those on the main stem. In this species, the petiole, midrib, veins and lamina are puberulous.

The inflorescence is similar to that of *E. lyrata* except that it is always carried above the surface of the soil. The axis of the spike in this form of *Elytraria* is also thicker than that of *E. lyrata*. In this form of *Elytraria* the three lateral lobes of the lower lip are rounded at the apex, not emarginate as in *E. lyrata* and slightly reflexed. The middle lobe is rounded and retuse; it is concave and up-turned in an open flower so that the three lobes do not lie in the same plane. The stamens of this form are different from those of *E. lyrata* in that the connective does not extend beyond the distal end of the anther cells. The style also, unlike that of *E. lyrata*, expands into a complanate lanceolate stigma. The capsule is similar to that of *E. lyrata*, but is not red-tinted at the tip. The seeds are also similar to those of *E. lyrata*.

E. maritima is a much branched, prostrate, creeping plant. It is a facultative perennial without any perennial rootstock (Fig. 3). After germination the epicotyl grows in length and bears the first whorl of normal leaves at the second node. But unlike E. marginata this internode attains a maximum length of only 1—2 cm. The apical bud then begins to develop directly into a spike. At this time, the vegetative branches begin to appear. The first to



arise are the two lateral branches from the axils of the cotyledonary leaves. These grow horizontally in opposite directions more or less at right angles to the main axis, bear a whorl of leaves at the end of 6-12 cm long naked internode and trail on the ground, producing adventitious roots from the surface of the internodes. This type of branching from the axils of the cotyledonary leaves is characteristic of E. maritima only. Shortly after this, or about the same time, 3-5 branches also appear from the axils of the leaves of the main stem at the second node. These follow the same pattern of growth as the branches from the axils of the cotyledonary leaves. Branching generally continues beyond the primary to the secondary and tertiary degrees usually following a dichasial pattern but with frequent suppression of one of the two axillary branches. Many of the branches trail on the surface of the soil and produce roots from the internodes. After fruiting, the spikes wither and the plant dies. But those of its branches with adventitious roots established in the soil persist. They become eventually separated from the parent plant and continue to grow by the development of new axillary branches. This type of vegetative reproduction and perennation by the progressive death at the older parts of the plant and growth at the younger is not known in the other kinds of Elytraria.

The leaves are more or less broadly elliptic, with a slightly crenate ciliate margin, and are not cuneate at the base. They are also conspicuously smaller than those of the other three kinds of Elytraria. Mature leaves have a size range of (35—) 40—50 (—55) mm long, and (22—) 25—29—(31) mm broad.

In this species, only one short spike is formed at each node of the much branched stem and varies from 80-90 mm in length. The spikes of this species are therefore much shorter than those of the other types of Elytraria.

The floral and capsule characters are broadly the same as those of E. marginata. The seeds of this species are larger than those of other types of

Elytraria.

Elytraria ivorensis is an acaulous annual herb with a basal rosette of obovate leaves, (2.5—) 5.0—9.0 (—13) cm long, (2—) 4—5.5 (—6.5) cm broad; apex obtuse, margin sub-entire, base cuneate or rounded, undulatecorrugate; lamina bullate, pubescent above, glabrous below; petiole and midrib villous above, pubescent below; secondary nerves pubescent above and below.

The inflorescence is up to 30 cm long, longer than that of any of the three types of Elytraria. Floral and seed characters are similar to those of E. marginata.

HYBRIDIZATION

The four kinds of Elytraria occur largely in separate areas. So far no plants suggestive of hybridization between them have been known in the field.

But in the green house and in the garden, hybrids were found. These plants appeared to be intermediate between *E. marginata* and *E. maritima* in the following characters:

I) Leaf size and shape

II) Branching pattern and stoutness.

III) Position of branches.

IV) Inflorescence length and branching and

V) Size of central lobe of lower lip.

But the most remarkable difference has been found in the fecundity of these plants. A large proportion of non-turgid or bad pollen has also been observed. This condition appears to throw light on the sterility of these plants.

Later, attempts were made to bring about artificial crossing. The spikes of the first three kinds of Elytraria were bagged in the afternoon of the day before artificial crossing. Early in the morning, between 5.45 and 7.00 a.m., when the flowers were beginning to open, the two stamens were removed by means of a pair of specially prepared fine forceps. The stigma of the emasculated flower was then dusted with pollen collected by means of a mounting needle from another flower of a desired kind. The bags were replaced after every single operation, and the forceps and needle sterilised in absolute alcohol before another flower was emasculated and artificially pollinated. Artificial pollination was effected in all the first three kinds of Elytraria in mating pairs. The mature seeds of the capsule of each pollinated flower were sown in separate boxes. The percentage germination was very good (80%). and the seedlings were later transferred into larger boxes. Among the adult plants obtained later, some showed features possessed by both paternal and maternal parents. Those suspected hybrids resembled those that arose spontaneously in the green-house and in the garden in mixed cultivation.

When later *Elytraria ivorensis* was obtained, similar breeding experiments were performed. The cross between *E. lyrata* on the one hand and the other three on the other hand, resulted in plants all of which resembled *E. lyrata* if the pollen of each of the three was dusted on the stigma of *E. lyrata*. When the pollen of *E. lyrata* was dusted on the stigma of each of the other three, the mature plants obtained resembled their maternal parents. Hybrids were obtained only when the last three were crossed in mating pairs.

The cross between *E. marginata* and *E. ivorensis* produced hybrids which were acaulous but possessed spathulate, glabrescent leaves. Hybrids obtained from crosses between *E. ivorensis* and *E. maritima*, were caulescent and resembled those obtained from crosses between *E. marginata* and *E. maritima*.

All the hybrids are sterile and it is only in rare cases that a mature viable seed was obtained in one capsule out of 100—150 capsules.

These results seem to show that the pollen grains of *E. lyrata* will not germinate on the stigma of the other three kinds of *Elytraria*.

Chromosome counts of each of the first three kinds of Elytraria have al-

ready been obtained by Morton (l. c.) from root-tips. He showed that although the diploid number in each case was 38, the chromosomes of *E. maritima* were "little more than half the size of those in the other two species". This size difference of the chromosomes is particularly interesting vis-a-vis their potentiality for hybridization. It is possible that the almost complete sterility shown by the spontaneous as well as artificially induced F_1 hybrids between *E. marginata*, *E. maritima* and *E. ivorensis* is due to differences in their chromosome size. The high 0 / 0 of aborted pollen grains in the flower of F_1 hybrids strongly suggest some kind of meiotic irregularity during microsporogenesis.

Work on chromosome counts of the four species is still in progress.

DISCUSSION AND CONCLUSION

Results of collateral cultivation of the four kinds of *Elytraria* obtained from Ghana and the Ivory Coast show that they maintain their normal morphological features and identities in cultivation in uniform neutral habitat, except that under experimental conditions, *E. marginata*, *E. maritima* and *E. ivorensis* show a degree of luxuriance which is not normally encountered in plants growing in their natural habitats.

A comparative study of the four kinds of plants shows that they differ from one another in a number of important features. In addition they also differ from one another in their habit, mode of branching, life-form, life-

span, their geographical distribution and ecological preferences.

As to the breeding relationships between these plants, it was observed that *E. lyrata* would not hybridize with any of the three. A complete reproductive barrier therefore exists between *E. lyrata* on the one hand and the other three, on the other.

The other three types are interfertile but their F₁ hybrids are sterile.

From all the above evidence, it seems clear that *E. lyrata*, *E. marginata*, *E. maritima* and *E. ivorensis* represent populations which differ from one another not only in several morphological and eco-geographical features, but also in the fact that each is isolated from the other by a reproductive barrier.

If a "species is an isolated group of individuals whose sum of characters tends to keep constant by natural in breeding" and if a species is morphologically definable in that it has a sum total of characters, and every individual within it has constant resemblances with every other individual within it and constant differences from every individual of other species, even when the individuals are grown under diverse conditions (Turrill, 1925, 1940) or if species are "... the smallest natural populations permanently separated from each other by a discontinuity in the series of biotypes", (Du Rietz, Sv. Bot. Tidskr. 24:333. 1930) then there seems to be no reason why each of the four kinds of *Elytraria* in question should not be regarded as a distinct species.

Even if a purely genetical criterion is applied for the definition of species, if species are "groups of actually or potentially natural populations which are reproductively isolated from other such groups (MAYR, 1940 upheld by A. Löve, Taxon 13:33. 1964) but which may or may not be morphologically distinct," then each of the *Elytrarias* in question is to be regarded as a distinct species. For in the present investigation, it has been found that each has a reproductive barrier with the other three. This latter feature takes away all force from any possible argument for subspecific status for the four.

It is therefore concluded that *Elytraria lyrata* and *E. marginata* are not conspecific (Heine l. c.) but are distinct species. Similarly *E. maritima* and *E. ivorensis* are distinct enough to merit specific status. These conclusions agree with the view adopted by MORTON (l. c.) for the first three of these taxa.

The citations for the first three species, therefore, should be as appear in

Morton (l. c.) viz.,

1. Elytraria lyrata VAHL, Enum. Pl. 1; 106 (1805).

2. Elytraria marginata VAHL, Enum. Pl. 1; 108 (1805).

3. Elytraria maritima J. K. Morton in Rev. Biologia 1:54 (1956).